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DIET AND FEEDING ECOLOGY OF THE VERMILION SNAPPER, *RHOMBOPLITES AURORUBENS* (CUVIER) FROM NORTH CAROLINA AND SOUTH CAROLINA WATERS

Churchill B. Grimes

ABSTRACT

The diet of 353 adult and large juvenile vermilion snapper (*Rhomboplites aurorubens*) collected throughout 1972 and 1973 off the coast of North Carolina and South Carolina consisted mostly of small pelagic organisms. By volume, small pelagic crustacea (ostracods, copepods, stomatopods, amphipods, euphausiids, shrimps, crabs and their larvae) made up 38% of the diet, cephalopods accounted for 37%, pelagic gastropods (pteropods, heteropods, and other opisthobranchs) composed 11%, fish constituted 8.5%, and miscellaneous items (pelagic polychaetes, coelenterates, ctenophores, salps, nematodes, colonial tunicates, and fish eggs) accounted for 5.5%. Variation in diet for different size groups of fish was apparent. By volume, small juveniles (< 100 mm TL) consumed 67% copepods, 10% nematodes, 5% polychaetes, 5% fish scales, 3% ostracods, 3% larval crabs, 3% radiolarians, and 3% fish eggs. Intermediate juveniles (100–175 mm TL) consumed 68% (by volume) fish scales, 14% copepods, 9% cephalopods, and 9% pelagic gastropods, indicating transition in diet toward adults. Scale eating or cleaning habits may be implied. Data inconclusively evinces nocturnal feeding. The pelagic nature of food items clearly demonstrates that vermilion snapper forage in the water column.

The vermilion snapper, *Rhomboplites aurorubens*, is the most frequently caught snapper (Lutjanidae) along the coast of North Carolina and South Carolina where in 1972 and 1974 it was the second most frequently angled species in the Carolina headboat[1] fishery which landed between 1.3 and 1.6 million pounds of demersal fishes (Huntsman, 1976). The species, one of the smaller lutjanids, attaining a maximum size of 66 mm total length (TL) and 2,800 g is distributed from North Carolina and Bermuda, throughout the Caribbean and Gulf of Mexico south to southeastern Brazil (Cervigon, 1966; Böhlke and Chaplin, 1968).

The purpose of this paper is to describe the foods and feeding habits of the vermilion snapper; to consider the relative importance of the various food categories; to examine variation in food habits with capture depth and fish size; and to place the species in an appropriate trophic category. The foods and feeding habits of the vermilion snapper are poorly known. Dixon (1975) reported preliminary results from examination of stomach contents of 16 fish.

MATERIALS AND METHODS

Study Area

The outer continental shelf of North Carolina and South Carolina, bounded by Cape Hatteras, N.C. and Charleston, S.C., provides two distinct habitats attractive to tropical and subtropical fishes. The more spectacular of the two zones, the shelf break zone (Struhsaker, 1969), occurs at depths of 55–183 m where the relatively flat continental shelf slopes abruptly downward becoming the continental slope. This is a rugged area of jagged peaks, precipitous cliffs and rocky ledges where reliefs of 15 m

[1] Headboats are vessels which anglers pay for a day's fishing on a per person (thus per "head") basis.

are not uncommon (Menzies et al., 1966; Macintyre and Milliman, 1970).

The less dramatic second habitat lies shoreward of the shelf break zone on the relatively flat shelf between depths of 26–55 m. Scattered over this area are numerous low rock ridges, outcroppings and coral patches.

Data Collection and Analysis

Digestive tracts were examined from 353 fish landed by hook and line in the recreational fishery or caught from the R/V ONSLOW BAY and R/V EASTWARD and some juveniles were trawled from R/V DOLPHIN. After capture the stomach and intestines were removed, labeled and preserved in 10% Formalin[2]. After at least 1 week, preserved materials were drained of Formalin, washed in tap water for several days, then placed in 70% isopropyl alcohol.

Later, the stomach and intestines were cut longitudinally and the contents placed in a bowl for examination using a binocular microscope. The degree to which each stomach was filled was estimated and expressed in percentage. Food items were identified to the most precise taxonomic level possible. Because many food items were too digested to permit identification, some taxa were combined to form 19 food categories (Table 1) for analysis and presentation of results.

The volume of each food item or group of identifiable items was determined by displacement in a graduated cylinder. Results were tabulated and presented as: (1) the percentage of the total volume of identifiable foods for each category and (2) the percentage frequency of occurrence of each category in all digestive tracts examined containing food.

In presenting results reference will be made to three size categories. Adults and large juveniles were > 175 mm TL, intermediate juveniles 100–175 mm TL and small juveniles < 100 mm TL.

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Composition of Diet

Although the diet varies somewhat with size, all sizes feed predominantly on small pelagic and epibenthic animals (Table 2). Small pelagic or epibenthic crustaceans made the largest contribution to bulk of the foods examined, collectively 38% by volume. Components were ostracods, cyclopoid and calanoid copepods, post-larval stomatopods or mantis shrimp, amphipods, euphausiid shrimp, natantian and reptantian decapods (portunid crabs) and their larvae (mysis, zoea, protozoea, megalopa and phyllosoma). Amphipods, mostly Hyperiidae, frequently occurred (43.8%) and made up the greatest bulk of any crustacean group (12.5% by volume). Natantian (swimming) decapods (penaeid or caridean shrimp) were the most frequently occurring crustacean group (45.6%); other groups occurring less frequently and accounting for less volume are given in Table 1.

Cephalopod mollusks (mostly squid) accounted for the largest portion (by volume) of the diet of any single food category (36.8%) and appeared in 34.1% of digestive tracts examined. Bait squid were distinguishable from normal foods because bait squid were rarely whole and possessed fish hook holes and cut edges. Pelagic gastropod mollusks (mostly heteropods and pteropods), pelagic polychaetes (Alcyopidae) and others accounted for less bulk and appeared less frequently (Table 1).

A plot of percent by volume against percent frequency of occurrence for each food category gives an indication of the relative significance of each category (Tester, 1932) (Fig. 1). This method weights volume and frequency of occurrence equally, thus cephalopods, amphipods, shrimps, pelagic gastropods, fish, and mantis shrimp are the most important food categories.

Most food items were quite small. When not represented by larvae, species were either naturally diminutive or represented by small juveniles (e.g., *Ovalipes quadulpensis*,

Table 1. Percentage by volume and percentage frequency of occurrence of food categories in digestive tract contents of vermilion snapper stratified according to season and capture depth (offshore ⩾30 fm or 55 m depth)

	Spring (n = 77)		Summer (n = 46)		Fall (n = 100)		Winter (n = 2)	
Food Categories	% vol.	% freq.	% vol.	% freq.	% vol.	% freq.	% vol.	% freq.
Coelenterates ctenophores and salps	2.4	11.7	0.9	4.4	0.9	2.0		
Nematodes	0.2	3.9	0	0	0.1	6.0		
Pelagic polychaetes	1.6	11.7	0	0	0.3	6.0		
Cephalopod mollusks	38.3	36.4	34.3	36.9	36.9	32.0		
Pelagic gastropods	8.1	18.2	23.7	10.9	1.3	6.0		
Ostracods	1.1	24.7	0.8	30.4	1.4	19.0	1.9	50.0
Copepods	0.1	2.6	0	0	1.9	11.0	0	0
Post-larval stomatopods	5.4	31.2	3.1	30.4	9.4	30.0	7.5	50.0
Amphipods	14.8	58.4	8.8	58.7	11.4	26.0	0.2	50.0
Euphausiids	0	0	<0.1	2.2	0	0	0	0
Natantian decapods	12.4	72.7	5.9	50.0	4.7	22.0	68.1	100.0
Larval natantian decapods	4.3	40.3	3.7	39.1	3.4	17.0	5.6	50.0
Reptatian decapods	3.5	9.1	0.2	2.2	1.7	9.0	0	0
Larval reptantian decapods	3.2	46.8	1.3	39.9	4.8	24.0	1.9	50.0
Colonial tunicates	0.7	3.9	9.4	8.7	0.4	2.0		
Larval fish	3.2	20.8	0.3	8.7	0.4	5.0		
Fish eggs	0.2	2.6	0	0	<0.1	1.0		
Adult and juvenile fish	0.7	3.9	7.6	26.1	20.5	16.0		
Fish scales	0	0	0	0	0.8	15.0		

	TOTAL		Offshore (n = 115)		Inshore (n = 64)	
Food Categories	% vol.	% freq.	% vol.	% freq.	% vol.	% freq.
Coelenterates ctenophores and salps	1.7	5.8	2.9	8.7	0.6	1.6
Nematodes	0.1	3.9	0.2	4.4	0.1	6.3
Pelagic polychaetes	0.9	6.6	1.2	10.4	2.1	4.7
Cephalopod mollusks	36.8	34.1	20.9	24.4	50.3	34.4
Pelagic gastropods	10.7	11.1	11.1	13.9	1.1	6.3
Ostracods	1.1	23.5	1.8	24.4	0.7	14.1
Copepods	0.5	5.8	0.4	3.5	1.3	9.4
Post-larval stomatopods	5.7	30.5	10.3	40.0	3.3	15.6
Amphipods	12.5	43.8	21.4	56.5	7.5	12.5
Euphausiids	<0.1	0.4	0	0	0	0
Natantian decapods	9.1	45.6	9.6	54.8	18.9	25.0
Larval natantian decapods	3.9	29.7	6.9	38.3	1.2	9.4
Reptatian decapods	2.2	7.5	1.2	8.7	6.6	6.3
Larval reptantian decapods	3.0	34.5	5.2	45.2	1.3	10.9
Colonial tunicates	2.9	3.9	2.9	6.1	0	0
Larval fish	1.8	11.1	3.1	16.5	2.3	4.7
Fish eggs	0.1	1.3	0.2	1.7	0	0
Adult and juvenile fish	6.8	13.7	0.7	2.6	1.7	4.7
Fish scales	0.2	6.6	0	0	0.9	23.4

Table 2. List of invertebrates and fish families identified from digestive tract contents of vermilion snapper

Invertebrates
Polychaetes
Alcyopidae
Serpulidae
Cephalopod mollusks
Lolliguncula brevis
Histioteuthis sp.
Octopus sp.
Gastropod mollusks
Tonna galea (*veliger*)
Sagatica semiculcata
Cymatium parthenopeum (*veliger*)
Oxygyrus keraudrenii
Carinaria sp.
Crustaceans
Ostracods
Calanoid copepods
Cyclopoid copepods
Oncaea sp.
Stomotopods
Squilla sp. (post-larvae)
Gammarid amphipods
Hyperiid amphipods
Brachycoelus sp.
Hemityphus sp.
Lestrigonus schizogeneois
Lycaea sp.
Oxycephalus clausi
Paracoelus sp.
Paratyphus sp.
Phronima sedentaria
Tetrathynus sp.
Natantian decapods
Acetes americanus
Leptochaela seratoribita
Lucifer faxoni
Scyonia brevirostris
Sergestes tenuiremis
Sergestes sargassi
Reptantian decapods
Scyllarus sp.
Ovalipes quadulpensis
Portunus ordwayi
Fishes
Ophichthidae—snake eels
leptocephalus larvae
Synodontidae—lizard fishes
Synodus sp.
Myctophidae—lanternfishes
Bregmacerotidae—codlets
Gadidae—codfishes
Urophycis sp.
Ophidiidae—cusk-eels and brotulas
Ophidion sp.
Holocentridae—squirrelfishes
Syngnathidae—pipefishes
Serranidae—sea basses
Centropristis sp.
Carangidae—jacks
Bramidae—pomfrets
Pterycombus brama
Labridae—wrasses
Hemipteronotus sp.
Stromateidae—butterfishes
Scorpaenidae—scorpion fishes
Triglidae—searobins
Bothidae—lefteye flounders
Solidae—soles
Cynoglossidae—tonguefishes
Balistidae—triggerfishes and filefishes
Ostraciidae—boxfishes
Tetradontidae—puffers

a portunid crab, mean carapace width = 28.9 mm; *Scyllarus* sp., Spanish lobster, mean TL = 18.9 mm; *Oncaea* sp., a cyclopoid copepod, mean TL = 0.68 mm; *Lolliguncula brevis*, squid, mean TL = 26.3 mm). Larval fish averaged about 12 mm in TL except for leptocephalus larvae which were as long as 80 mm. Juvenile and small adult fish ranged from 35 to 120 mm TL. Polychaetes were represented only by fragments, but estimated reconstructed length is as long as 110–120 mm. Largest free-living nematodes were only about 20 mm long.

Variations in Diet

Diet varies with size of fish (Fig. 2). In the smallest individuals (< 100 mm TL) copepods (67% by volume) and nematodes (10% by volume) constituted the bulk of the diet; and in intermediate juveniles (100–175 mm TL) fish scales (68% by volume) and copepods (14% by volume) were the two most important food types. At 100–175 mm TL juveniles began to eat pelagic gastropods (9% by volume) and cephalopods (9% by volume). The smallest juveniles (< 100 mm TL) fed primarily on copepods, the smallest "small pelagic crustaceans" consumed by adults. Ostracods and larval crabs were also eaten by the smallest juveniles as

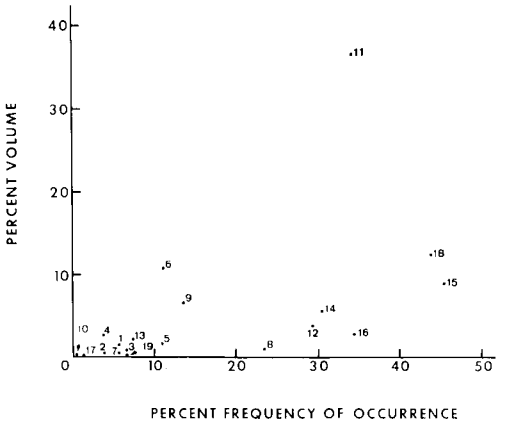

Figure 1. Significance plots (Tester, 1932) for 19 categories of adult and large juvenile vermilion snapper foods. Numbers indicate the food category for that plot (1 = coelenterates, ctenophores and salps; 2 = nematodes; 3 = pelagic polychaetes; 4 = colonial tunicates; 5 = larval fish; 6 = pelagic gastropod mollusks; 7 = copepods; 8 = ostracods; 9 = fish; 10 = euphausiid shrimp; 11 = cephalopod mollusks; 12 = larval shrimp; 13 = reptantian decapods; 14 = larval stomatopods; 15 = natantian decapods; 16 = larval crabs; 17 = fish eggs; 18 = amphipods; 19 = radiolarians and fish eggs).

well as large juveniles and adults. Ostracods were 3.3% of the volume for smallest juveniles and 1.1% for large juveniles and adults; larval crabs composed 3.3% of the volume in smallest juveniles and 3.0% for large juveniles and adults.

There may be seasonal variation in diet. Pelagic Crustacea (ostracods, copepods, stomatopods, amphipods, euphausiids, shrimp, larval shrimp, crabs, and larval crabs) composed the highest percent of volume of digestive tract contents in spring (March, April, and May), 44.7%; lowest in summer (June, July, and August), 23.7%; and increasing in fall (September, October, and November), 38.6%. The percent by volume of cephalopods remained nearly constant seasonally (Table 1) but pelagic gastropods varied from 8.1% in spring to 23.7% in summer to 1.3% in fall. Seasonal values for fish (larval and juvenile) were 3.9% in spring, 7.9% in summer and 20.8% in fall. Other categories also showed variation (Table 1).

An analysis of the relationship of diet to depth indicates several trends (Table 1). Small pelagic crustaceans comprise a larger percentage of the volume of gut contents offshore (> 55 m, or 30 fm depth) than inshore (< 55 m or 30 fm depth); 56.6% compared to 40.9%. Cephalopods accounted for less volume offshore (20.9%) than inshore (50.3%). Conversely, pelagic gastropods constituted 11.1% by volume of digestive tract contents from offshore fish samples compared to 1.1% of the volume of inshore samples. Percentage by volumes of fish were approximately equal for both depth regimes (Table 1) but coelenterates, ctenophores and salps and colonial tunicates were higher offshore (Table 1).

Specimens were collected during both daylight and darkness and comparison of results may demonstrate diel feeding periodicity. Mean percentage fill for fish sampled during daylight was 21.6% as opposed to 24.9% for fish taken during darkness (N = 176). These data may indicate that slightly more feeding occurs at night, however, the means are not significantly different ($p = 0.582$).

The percentages of stomachs with and without contents were also considered. For fish collected during daylight 23 had empty stomachs and 62 stomachs contained food; likewise for fish sampled at night, 16 had empty stomachs and 75 contained food. A test for quality of two percentages (Sokal and Rohlf, 1969) used to determine the significance of the proportions of empty stomachs in day versus night collections indicated that percentages are not significantly different ($p = 0.128$).

Even though catch-per-unit-effort data for dark and light periods were not kept, after several years of sampling for vermilion snapper it is apparent that fishing is appreciably better during darkness. This may not reflect increased feeding activity at night but rather lessened ability of fish to avoid capture.

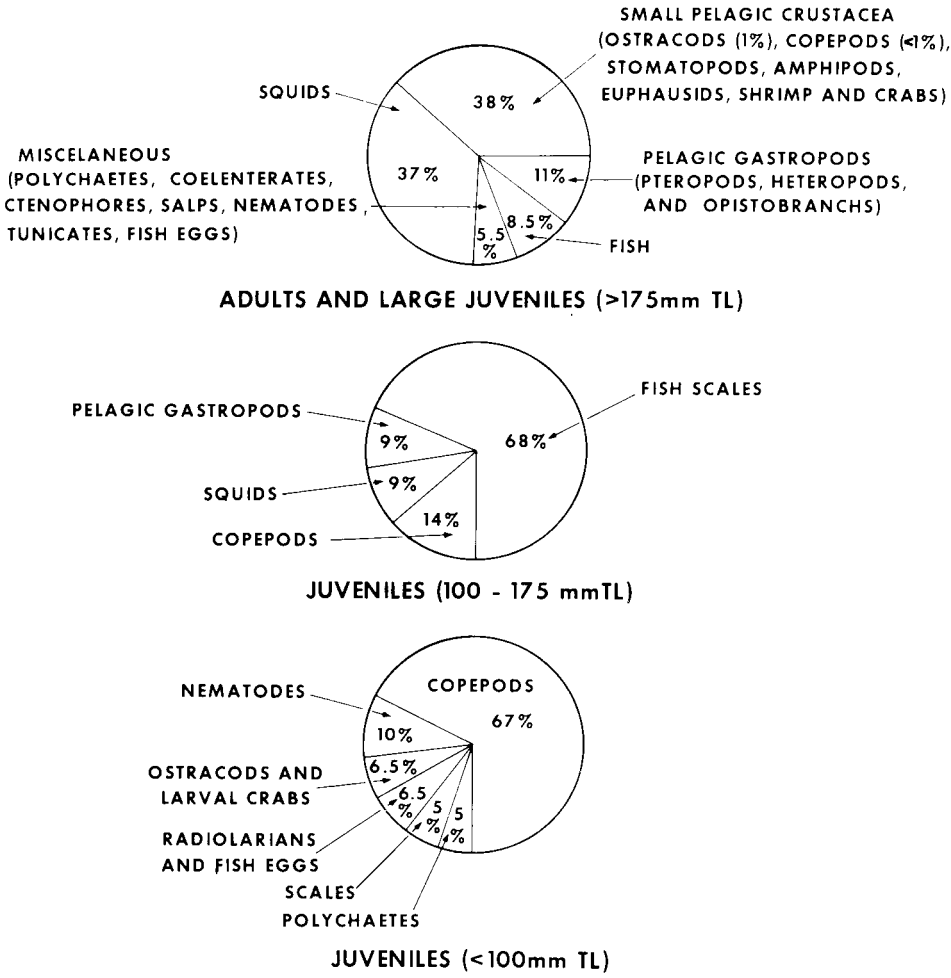

Figure 2. Percentage volume of stomach contents made up of various food categories for three size groups of vermilion snapper. (Spelling in above figure should be opisthobranchs.)

Discussion

Results mostly indicate actual proportions of foods in the diet of vermilion snapper. However, coelenterates, ctenophores, and salps may occur in larger proportions than results imply. Their gelatinous consistency made them difficult to distinguish and hyperiid amphipod genera *Lestrigonus*, *Phronima*, and *Vibilia*, identified from digestive tract contents, are known symbionts with leptomedusae, siphonophores, and salps (Bowman and Gruner, 1973).

Most food organisms making up the diet may be characterized as pelagic, planktonic or epibenthic (Barnes, 1968; Hobson and Chess, 1976). In contrast, food studies on other western Atlantic species of snapper (*Lutjanus campechanus*, *L. griseus*, *L. apodus*, *L. analis*, *L. jocu*, *L. synagris*, *L. vivanus*, *L. buccanella*, *L. purpureus*, *L. cyanopterus*, and *L. mahogoni*) show them to feed on predominantly benthic fishes, crabs, shrimps, octopods, and occasionally gastropods and annelids (Bradley and Bryan, 1974; Brownell and Rainey, 1971; Croker,

1962; Evermann and Marsh, 1902; Longley and Hildebrand, 1941; Mosley, 1966; Randall, 1967; Starck and Schroeder, 1970). However, Longley and Hildebrand (1941) report the diet of the yellowtail snapper, *Ocyurus chrysurus*, to consist of small fishes, small shrimps, stomatopods, and annelids and Randall (1967) found (by volume) 15% crabs and larvae, 16% pteropods, and several other lesser important categories of mostly "pelagic" organisms. Evidently the vermilion and the yellowtail snapper represent a divergence in food habits from many other snappers.

Fishes that exploit small forms of pelagic and planktonic or epibenthic food sources have been variously referred to as "planktivores," "particulate plankton pickers," "fusiliers," "carnivores in mid-winter," "hoverers" or "foragers in the water column" (Hobson, 1965, 1968, 1973, 1975; Starck and Davis, 1966; Collete and Talbot, 1972). Davis and Birdsong (1973) discuss this method of food resource utilization and point out morphological convergences which have occurred among different perciform families and cite the yellowtail snapper as an example of the water column forager. The vermilion snapper equally exemplifies this life mode. Like Davis and Birdsong's (1973) examples, it possesses the appropriate external features of lunate caudal fin, terete body form including sharp profile of head and nose, fin squamation, large eye diameter relative to head size, fine extensive dentition, terminal mouth, long numerous gill rakers, and long premaxillary processes with great protrusibility.

There are obvious differences in the diet of different size fish. Adults and large juveniles, intermediate juveniles and small juveniles all consumed predominantly pelagic, planktonic, or epibenthic organisms but the smallest juveniles concentrated on the more diminutive varieties (i.e., 67% volume copepods). Intermediate size juveniles relied less upon copepods (14% volume) and began to feed upon cephalopod mollusks (9%) and pelagic gastropods (9%), indicating a transition in their diet toward that of adults and large juveniles. These variations in diet with size may also imply changing feeding periodicity with size. The preponderance of diurnally active copepods in the guts of smallest juveniles suggests diurnal feeding. Hobson and Chess (1976) draw this conclusion from similar food data for some southern California planktivorous fishes.

Small juveniles of other snappers also feed primarily on small planktonic and pelagic animals but their diets change drastically with growth in favor of larger mostly benthic organisms. In gray snapper (*L. griseus*), Starck and Schroeder (1970) found that copepods and amphipods were important only in fish less than 50 mm standard length (SL); with increasing size, these crustaceans decreased in dietary importance and crabs and fish became abundant in larger fish. Red snapper (*L. campechanus*) less than 150 mm SL eat amphipods, copepods, leptocephalus larvae, fish larvae, and other zooplankters (Bradley and Bryan, 1974). Between 101–150 mm SL food emphasis shifts from zooplankton to juvenile crustaceans and fishes.

That fish scales constitute 68% of the volume of the diet of intermediate size juveniles (100–175 mm TL) suggests scale eating or cleaning habits as has been shown for other juvenile warm-water species (e.g., *Diplodus holbrooki* and *Oligoplites saurus*) (Hoese, 1966; Carr and Adams, 1972; Major, 1973). Among contents other than scales there were no identifiable ectoparasites. Although inconclusive (only 22 juvenile specimens < 175 mm examined), the evidence suggests scale eating as one explanation.

Diet apparently varies somewhat with season and depth. Bradley and Bryan (1974) report only slight seasonal variation in foods of adult red snapper, *L. campechanus*, from the Gulf of Mexico. Starck and Schroeder (1970) found substantial differences in food habits of gray snapper (*L. griseus*) captured at different depths but the depth differences accompanied appreciable differences in com-

munity structure. The slight observed variations probably reflect variations in available foods but necessary comparative data on community structure were not obtained.

Hobson (1965, 1973, 1975), Davis and Birdsong (1973), Starck and Davis (1966), Hobson and Chess (1976) and other authors discuss the feeding ecology of planktivorous fishes and agree that as adults most are either nocturnal or diurnal feeders with very little overlap. Results inconclusively indicate that vermilion snapper feed nocturnally, and temporal activity patterns of food organisms (Table 2) lend additional credence to this hypothesis. Shrimps of the genus *Sergestes* are known to be active nocturnally (Crosnier and Forest, 1973). Another small shrimp and food item, *Lucifer faxoni*, is reported to be active at night (Hardy, 1956). Hobson and Chess (1976) state that polychaetes; ostracods; amphipods; euphausiids; caridean shrimp larvae, adults and juveniles; reptantian zoea and megalopa (all vermilion snapper foods) are more abundant nocturnally in shallow water communities in southern California.

Many other snappers feed almost exclusively during the night (Hobson, 1965; Longley and Hildebrand, 1941; Randall, 1967; Starck and Schroeder, 1970). Davis and Birdsong (1973) state that "feeding, either diurnally or nocturnally, is more often phylogenetically correlated to the family level." Pigmentation is red in the vermilion as well as in several other snappers (*L. campechanus*, *L. vivanus* and *L. buccanella*) known to be nocturnal, although benthic, foragers.

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